

THE LARVAL AND POSTLARVAL DEVELOPMENT OF *PARTHENOPE SERRATA* REARED IN THE LABORATORY AND THE SYSTEMATIC POSITION OF THE PARTHENOPINAE (CRUSTACEA, BRACHYURA)¹

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According to Rathbun (1925), *Parthenope (Platylambrus) serrata* (H. Milne Edwards) has a range extending from the Bermudas, and Cape Hatteras, North Carolina, through the Gulf of Mexico and Bahama Islands, to Bahia, Brazil. The known substrate on which it occurs consists of sand, broken shells, gravel, corals or combinations of these. Holthuis (1959) found ovigerous females in Surinam from May to June. Williams (1965), citing the United States National Museum records, said ovigerous females have been collected during June in North Carolina, summer in Florida, and October in Cuba.

The studies of larval development of parthenopid crabs have been limited to the first zoeal stage or planktonic materials, and have dealt mostly with Mediterranean species. Gourret (1884) first mentioned the zoeae of *Parthenope massena* (Roux) (which he indicated with the name *Lambrus massena*). Cano (1893) described and illustrated three zoeal stages and Boraschi (1921) illustrated a telson of *Parthenope* species (as *Lambrus* sp.). Bourdillon-Casanova (1960) described and illustrated the first two zoeal stages of *P. massena* (as *L. massena*). Heegaard (1963) hatched and described the first zoeal stages of *P. massena* and *P. angulifrons* Latreille (as *L. massena* and *L. angulifrons*), presenting a color plate to show the chromatophore patterns. Aikawa (1937) described the first zoea of the Japanese species *P. valida* De Haan (as *L. validus*) reared from hatching. The present work is the first study of the complete larval and post-larval development of any species of the Parthenopidae, based on reared animals.

Since Milne Edwards' (1834) definition of family Oxyrhinques (=Oxyrhyncha), all major workers of Oxyrhyncha (e.g., Dana, 1851; Miers, 1879; Alcock, 1895; Rathbun, 1925; Sakai, 1938; Balss, 1957; Garth, 1958) have placed the Parthenopidae under Oxyrhyncha.

MATERIALS AND METHODS

Two ovigerous females used in the present work were collected by a Biscayne Bay shrimp trawler on 4 March, 1965. These were kept in a running sea-water aquarium with sand. When eye spots appeared in the eggs each ovigerous female was then placed into a 25-cm diameter finger bowl of clear plastic with filtered

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Biscayne Bay water. The females were fed cut shrimp and the water was changed daily. Hatching occurred on 13 March and 4 April, 1965.

After hatching, each larva was coded with a serial number and placed singly in a compartment of a plastic culture box. Each hatch consisted of 90 larvae reared at 25° C; 35 larvae from the first brood and 45 larvae from the second brood were reared at 20° C. Each compartment contained about 20 cc of filtered Biscayne Bay water. The first three zoeal stages were fed the smallest nauplii of just-hatched *Artemia* eggs, obtained by filtering through stainless steel screen (105 × 105 mesh, 0.0003 inch wire). The later zoeal and megalopal stages were fed unfiltered newly hatched *Artemia*. Chopped fresh shrimp was fed to the early stage crabs. Animals were changed to compartments with clean seawater, fed fresh food daily and were checked for molted and dead individuals. Salinity range of the rearing seawater was 34–37‰.

Exuviae and specimens of each developmental stage were preserved in 7% buffered formalin. These were stained with Mallory's acid fuchsin red or chlorazol black. The larval appendages for drawing were dissected in 85% lactic acid, while crab appendages were dissected in full strength ethylene glycol. The appendages after drawing were mounted permanently in Turtox CMCS, a stained water miscible mounting medium. Drawings were made with aid of a camera lucida. Details of the appendages were checked under high power (400× or more). Four specimens of each stage were measured with a calibrated ocular micrometer. The carapace length of zoeae was measured in lateral profile from the anterior margin of the ocular peduncle to the extremity of the posterior margin of the carapace. Carapace length of megalopa and crab were measured dorsally from the tip of the rostral spine to the posterior margin of the carapace, and the width was measured across the widest part of the carapace. The size given for each stage is the arithmetic average of four specimens examined. The formulae for order of setation denote the number of setae from the proximal to the distal segment (or group) and was also based on four specimens.

The female crabs are deposited in the museum of the Institute of Marine and Atmospheric Sciences of the University of Miami (UMML 32-3356 and UMML 32-3582).

MORPHOLOGICAL RESULTS

The number of zoeal stages through which *Parthenope serrata* passes to reach the megalopa is five or six. Most individuals surviving to the crab stage had passed through six zoeal stages. The text figures provided are as accurate as possible, hence the text is mainly restricted to comments on features not obvious from the figures or to emphasize any variations that were found.

First zoea (Fig. 1)

Carapace: Length approximately 0.37 mm. Dorsal, rostral and lateral spines as illustrated. Forehead rounded, with muscle bands plus a small protuberance. No anterior seta, nor infero-lateral setae present. A seta on each postero-lateral part of dorsal spine. Eye sessile with minute ocular papillae. *Abdomen*: Lateral knobs, postero-lateral process as shown. *Telson*: Lunate, bearing a dorsal spine

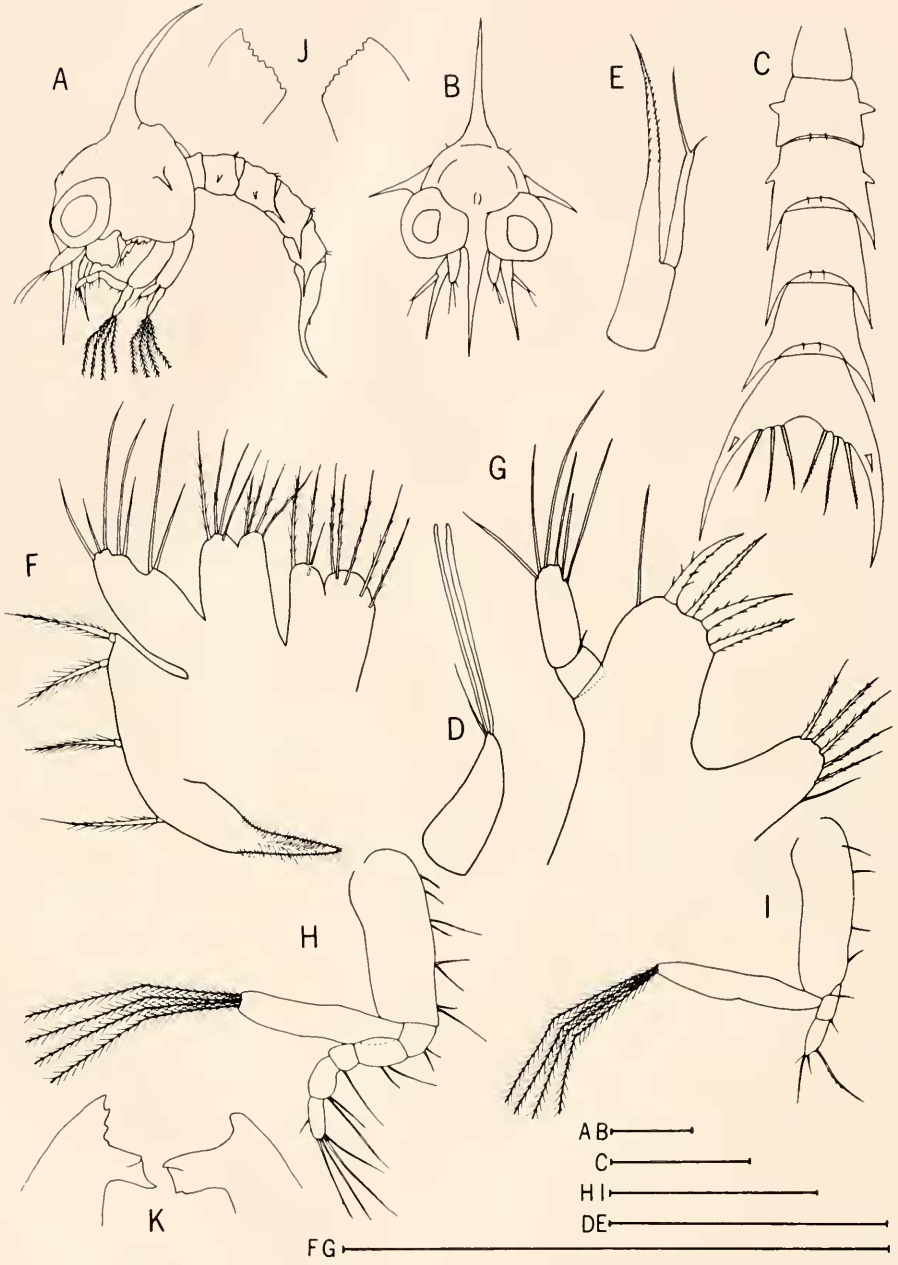


FIGURE 1. *Parthenope serrata*: First zoea; A, lateral view; B, anterior view of carapace; C, abdomen; D, antenna 1; E, antenna 2; F, maxilla 2; G, maxilla 1; H, maxilliped 1; I, maxilliped 2; J, antero-ventral view of mandible; K, postero-median view of mandible. Bar scales represent 0.2 mm.

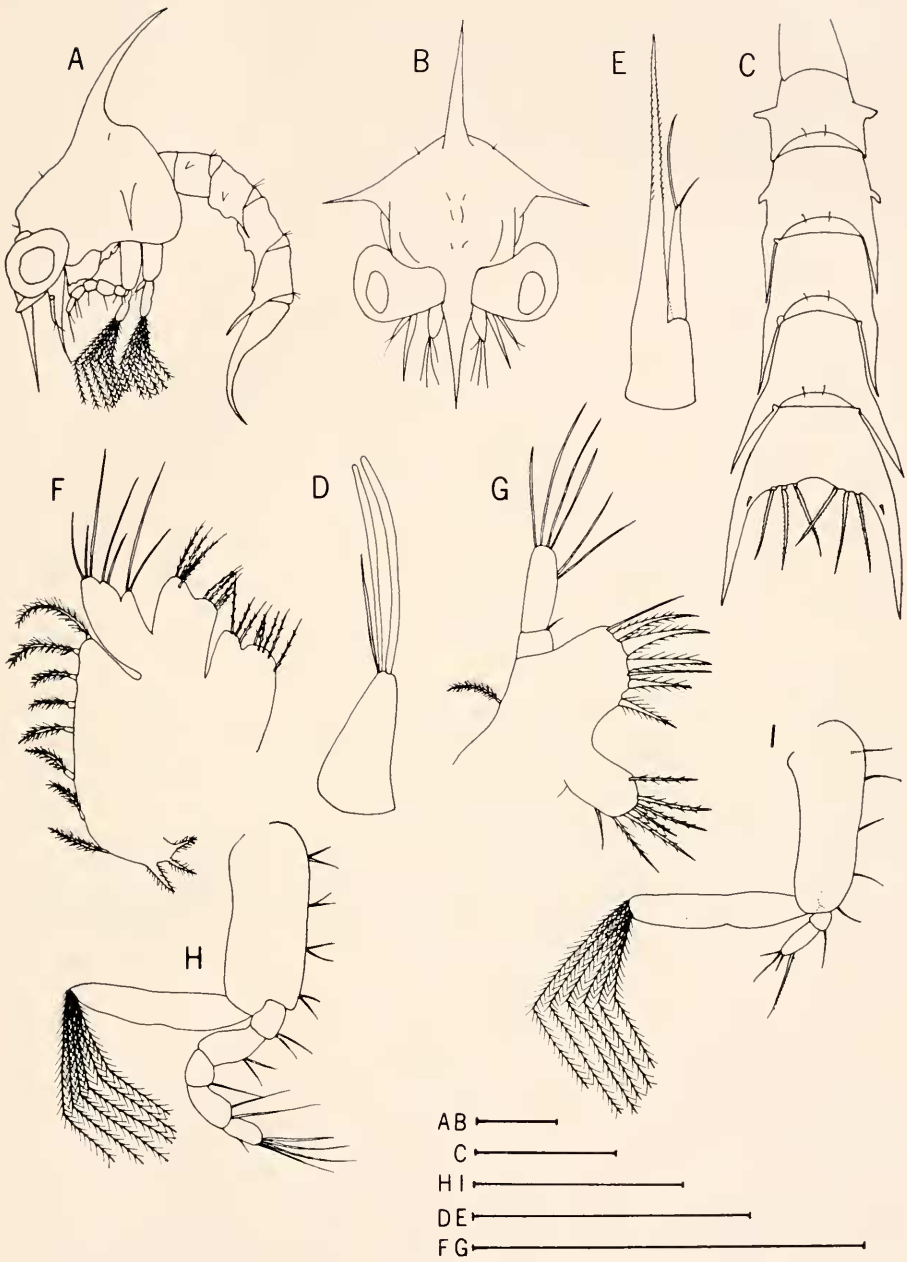


FIGURE 2. *Parthenope serrata*: Second zoea; A, lateral view, B, anterior view of carapace; C, abdomen; D, antenna 1; E, antenna 2; F, maxilla 2; G, maxilla 1; H, maxilliped 1; I, maxilliped 2. Bar scales represent 0.2 mm.

on each fork. Occasionally a minute setule present on lateral margin of telson halfway to fork, visible only under high magnification (400×). *Mandible*: Nine to ten teeth on antero-ventral margin, three teeth on right postero-medial margin (none on left). *Maxilliped 1*: Endopodite, five-segmented, setae arranged (2, 2, 1, 2, 5). *Color*: Melanophores located on dorsal basal area of each lateral spine; on posterior basal part of dorsal spine; postero-ventral portion of carapace; on each mandible; on each side of the ventral surface of abdominal somites 1-5; on basal part of antenna 2. Inconspicuous melanophore located on interorbital area of rostrum and at middle part of basipodite of maxilliped 1. Eye a light yellow-green. *Pereiopods*: Buds present, minute.

Second zoea (Fig. 2)

Carapace: Length approximately 0.48 mm. Eyes stalked. In subsequent stages dorsal spine continually shortens in relation to carapace length and anterior base thickens. Four setae added on forehead, plus five hairs along infero-lateral margin. *Abdomen*: Lateral process of somites 3-5 more elongated. *Telson*: Inner margin less lunate than zoea 1. Dorsal spine on fork now reduced. *Maxilla 1*: A plumose seta added to (proximal to) endopodite. Basal and coxal endites each with increased number of setae. *Maxilla 2*: Scaphognathite setae increased to approximately eight; apical process now divided into three. *Maxillipeds 1 and 2*: Now with six natatory setae.

Third zoea (Fig. 3)

Carapace: Length approximately 0.59 mm. Forehead and anterior base of dorsal spine nearly a straight line. Additional setae added below forehead protuberance. Groove forming in proximal portion of rostral spine between eyes. *Abdomen*: Somite 6 now separated from telson. A pair of mid-dorsal setae on somite 1 (one seta in some individuals). *Antenna 1*: One small aesthetasc added. *Antenna 2*: Small endopodite bud appears. *Maxilla 1*: Basal endite now with nine setae. *Maxilla 2*: Space between three processes of endopodite noticeably increased. Scaphognathite with approximately 10 setae in addition to apical processes. *Maxillipeds 1 and 2*: Eight natatory setae. *Maxilliped 1*: Setae now arranged (2, 2, 1, 2, 6).

Fourth zoea (Fig. 4)

Carapace: Length approximately 0.66 mm. Lateral spines further reduced. Rostral spine at interorbital area well grooved. *Abdomen*: Somite 1 usually with three mid-dorsal setae. *Telson*: Dorsal spine on fork now minute. *Antenna 2*: Endopodite bud elongated. *Maxilla 2*: Scaphognathite usually with 14 plumose setae plus three to five divided apical processes. *Maxillipeds 1 and 2*: Eight and nine natatory setae, respectively. Occasionally these numbers reversed; or rarely eight on both. *Pereiopods*: Buds elongated and easily seen. *Pleopods*: Bud primordia recognizable.

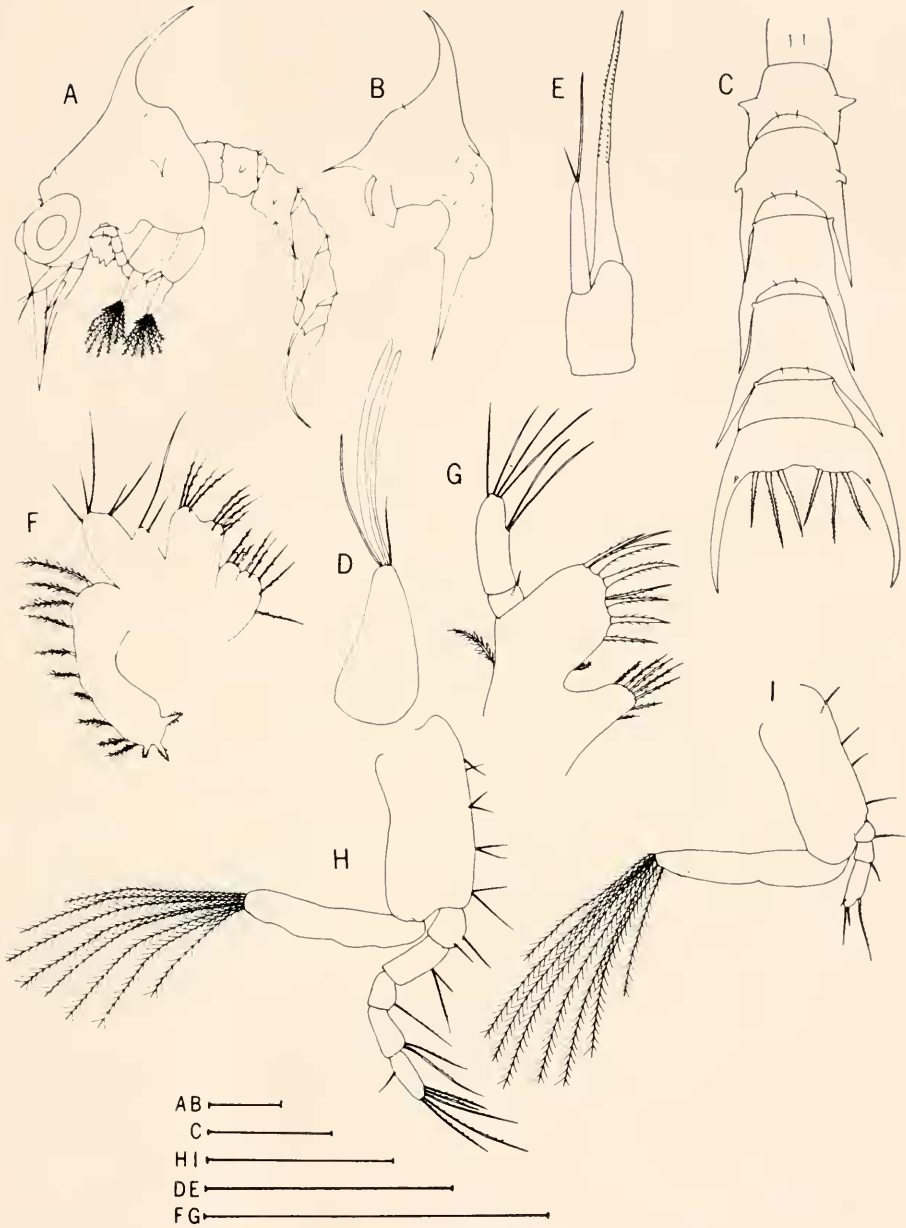


FIGURE 3. *Parthenope serrata*: Third zoea; A, lateral view, B, antero-lateral view of carapace; C, abdomen; D, antenna 1; E, antenna 2; F, maxilla 2; G, maxilla 1; H, maxilliped 1; maxilliped 2. Bar scales represent 0.2 mm.

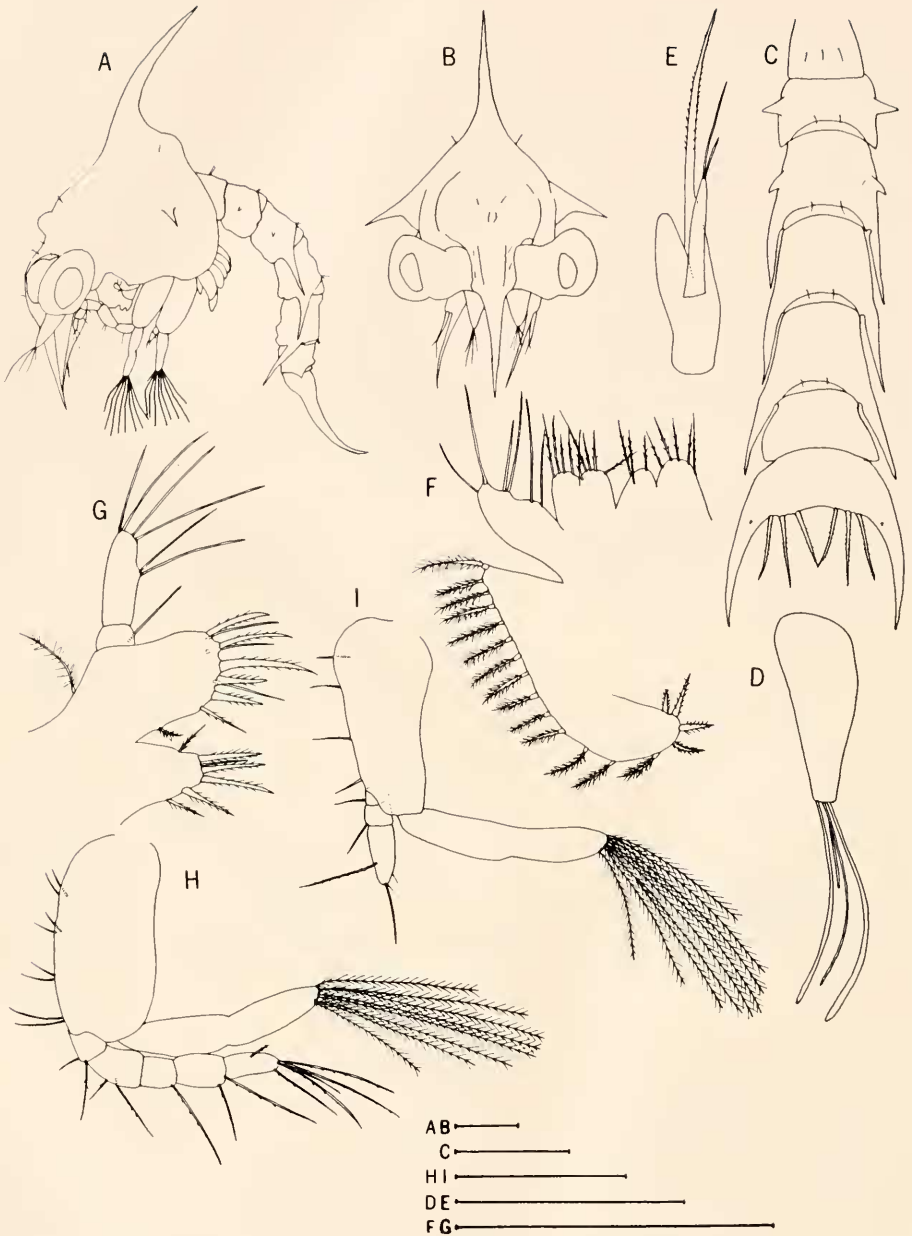


FIGURE 4. *Parthenope serrata*: Fourth zoea; A, lateral view; B, antero-lateral view of carapace; C, abdomen; D, antenna 1; E, antenna 2; F, maxilla 2; G, maxilla 1; H, maxilliped 1; I, maxilliped 2. Bar scales represent 0.2 mm.



FIGURE 5. *Parthenope serrata*: Fifth zoea; A, lateral view; B, antero-lateral view of carapace; C, abdomen; D, antenna 1; E, antenna 2; F, maxilla 2; G, maxilla 1; H, maxilliped 1; I, maxilliped 2. Bar scales represent 0.2 mm.

Fifth zoea (Fig. 5)

Carapace: Length approximately 0.79 mm. General form more depressed than previous stages along with more stout and shorter dorsal spine. Two small setae on infero-lateral margin; a few minute setae posterior to these on future branchiostegite membrane. *Abdomen*: Somite 1 with approximately four



FIGURE 6. *Parthenope serrata*: Sixth zoea; A, lateral view; B, antero-lateral view of carapace; C, abdomen; D, antenna 1; E, antenna 2; F, maxilla 2; G, maxilla 1; H, maxilliped 1; I, maxilliped 2. Bar scales represent 0.2 mm.

dorsal setae. *Telson*: Dorsal spine on fork now rudimentary. *Antenna 1*: Six terminal, two (rarely one) subterminal aesthetascs. Distal position anticipates segmentation. Inner flagellum bud appears on medial margin. *Antenna 2*: Endopodite bud now extends beyond exopodite. *Maxillipeds 1 and 2*: Usually ten natatory setae each. *Pereiopods*: Buds enlarged, chelation beginning. *Pleopods*: Buds much elongated. *Gills*: Buds now visible.

Sixth zoea (Fig. 6)

Carapace: Length approximately 1.01 mm. More depressed; dorsal spine stouter, inclined more posteriorly than previous stage. Lateral spine much shorter. Rostrum thickened, with median ridge on proximal portion plus two setae. *Abdomen*: With approximately five mid-dorsal setae on somite 1. *Antenna 1*: Peduncle, inner flagellum, and dorsal flagellum differentiated. Partly segmented peduncle with a dorsal indentation. Dorsal flagellum with three groups of aesthetascs placed (5, 5, 2). *Antenna 2*: Endopodite remarkably elongated plus two terminal setae; anticipating segmentation. *Mandible*: Anterior proximal portion with a palp bud. *Maxilla 1*: Form remains unchanged from second zoeal stage but setae increase in number. *Maxilla 2*: Scaphognathite with approximately 23 setae; with branched apical processes. *Maxilliped 1*: Ten natatory setae. Basipodite setae increased (2, 2, 3, 3). *Maxilliped 2*: Eleven natatory setae. *Pereiopods*: Buds well developed. Chelae almost formed. *Pleopods*: Elongated, with terminal setae. *Gills*: Buds continue forming in respective locations; in exuviae they appear to be laminated.

Megalopa (Figs. 7, 8)

Carapace: Length approximately 1.47 mm; width 0.98 mm. Medial portion of rostrum at interorbital region slightly depressed. Gastric region moderately inflated and without protruding ridges as in majiid megalopae. Hepatic lobe a hemisphere. Cardiac spine (dorsal spine in zoeal stages) with few minute setae. *Abdomen*: Six somites plus telson; setation as shown. *Antenna 1*: Peduncle three-segmented; dorsal portion of proximal segment concave, supporting proximal portion of eye peduncle with expanded lateral margin. Segmentation between distal and penultimate segments of outer flagellum unclear. *Antenna 2*: No modifications on distal portion of basal article (such as in majiid megalopae). *Mandible*: Now with two-segmented palp. *Maxilla 2*: Apical processes of scaphognathite now bushy plumose setae, similar in form to marginal setae. A few setae on dorsal and ventral surface of scaphognathite. Endopodite with added lateral plumose setae. *Maxilliped 1*: Shape now radically changed; epipodite now fringed with seven or more smooth hairs. *Maxilliped 2*: Epipodite bud with one or two terminal setae. *Maxilliped 3*: As illustrated. *Pereiopods*: Sparsely covered with setae. Right cheliped slightly larger than left. Dactyl of pereopod 5 with long subterminal hair (=feeler); hair tip hook-shaped. *Pleopods*: Present on somites 2-6, natatory setae arrangement on exopodite progressing distally as follows: 13, 14, 13, 10, 4. Numbers of natatory setae inconsistent, varying considerably between specimens, and on different sides of same individual. Appendix interna usually with three hooks.

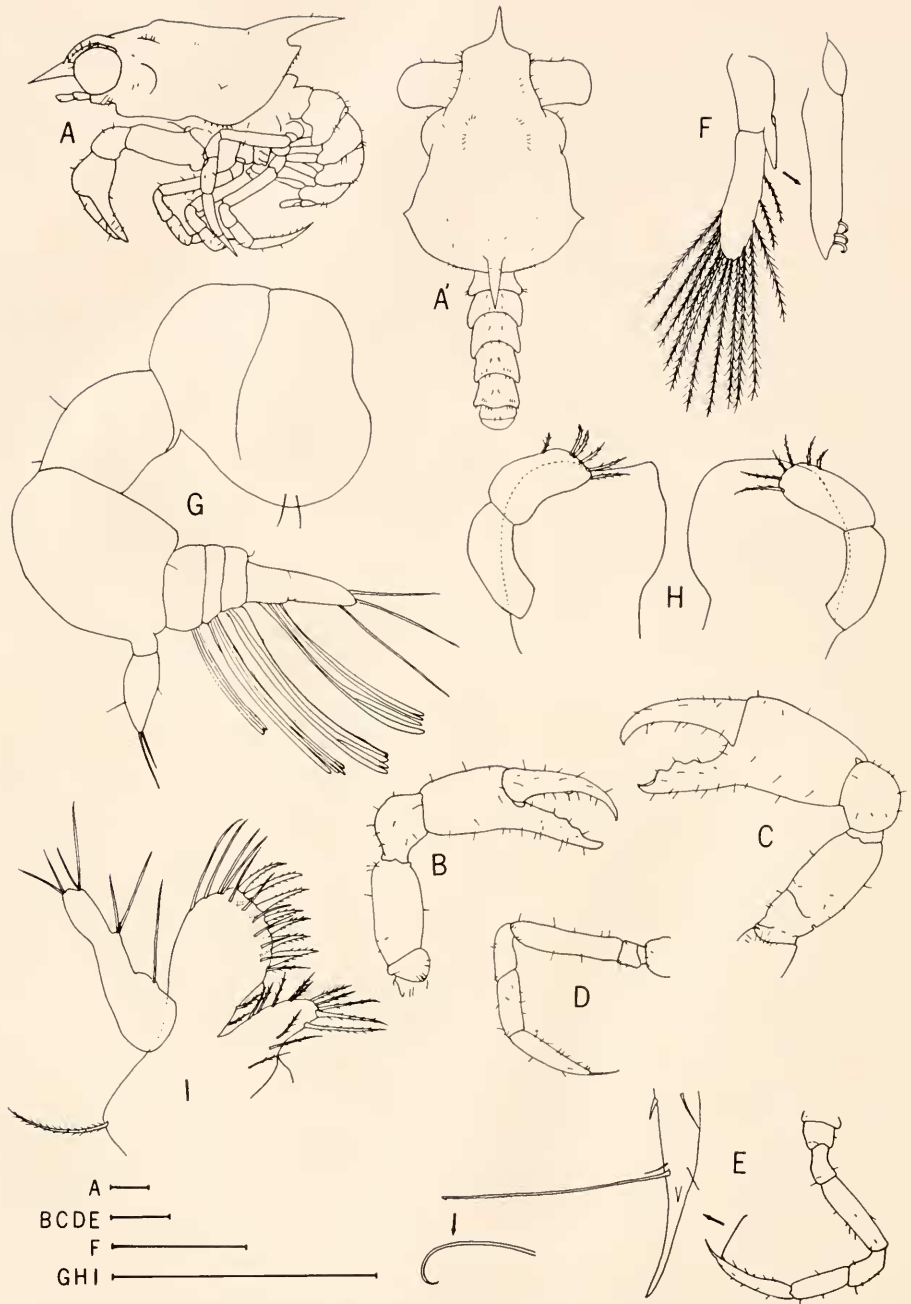


FIGURE 7. *Parthenope serrata*: Megalopa A, lateral view; A', dorsal view; B, left cheliped; C, right cheliped; D, pereopod 2; E, pereopod 5; F, pleopod; G, antenna 1; H, mandible; I, maxilla 1. Bar scales represent 0.2 mm.

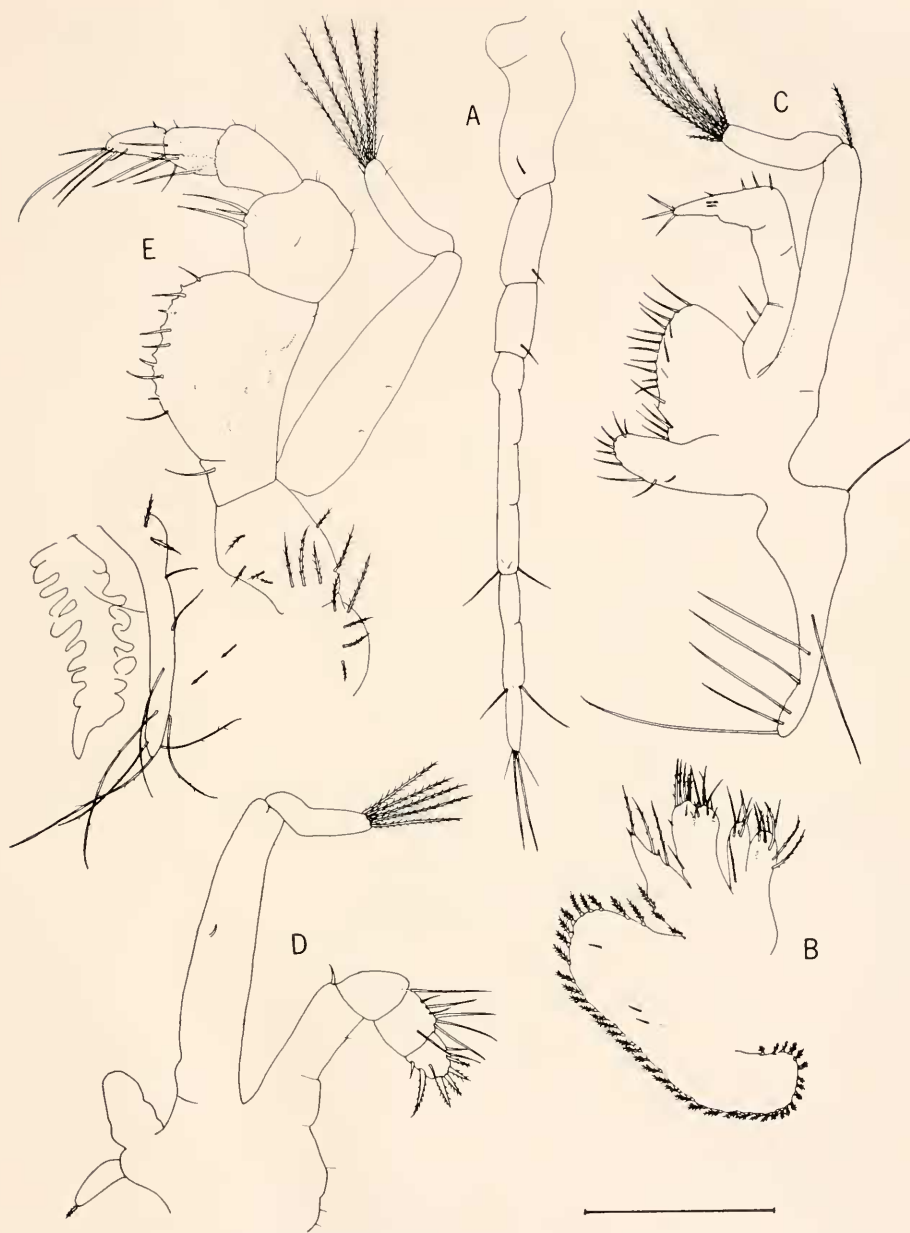


FIGURE 8. *Parthenope serrata*: Megalopa; A, antenna 2; B, maxilla 2; C, maxilliped 1; D, maxilliped 2; E, maxilliped 3. Bar scale represents 0.2 mm.

Gills: Development more advanced than in majiid megalopae. Maxilliped 2 with one elongate bud of future podobranch, incipient epipodite with two minute distal hairs. Maxilliped 3 with well laminated posterior arthrobranch, elongate

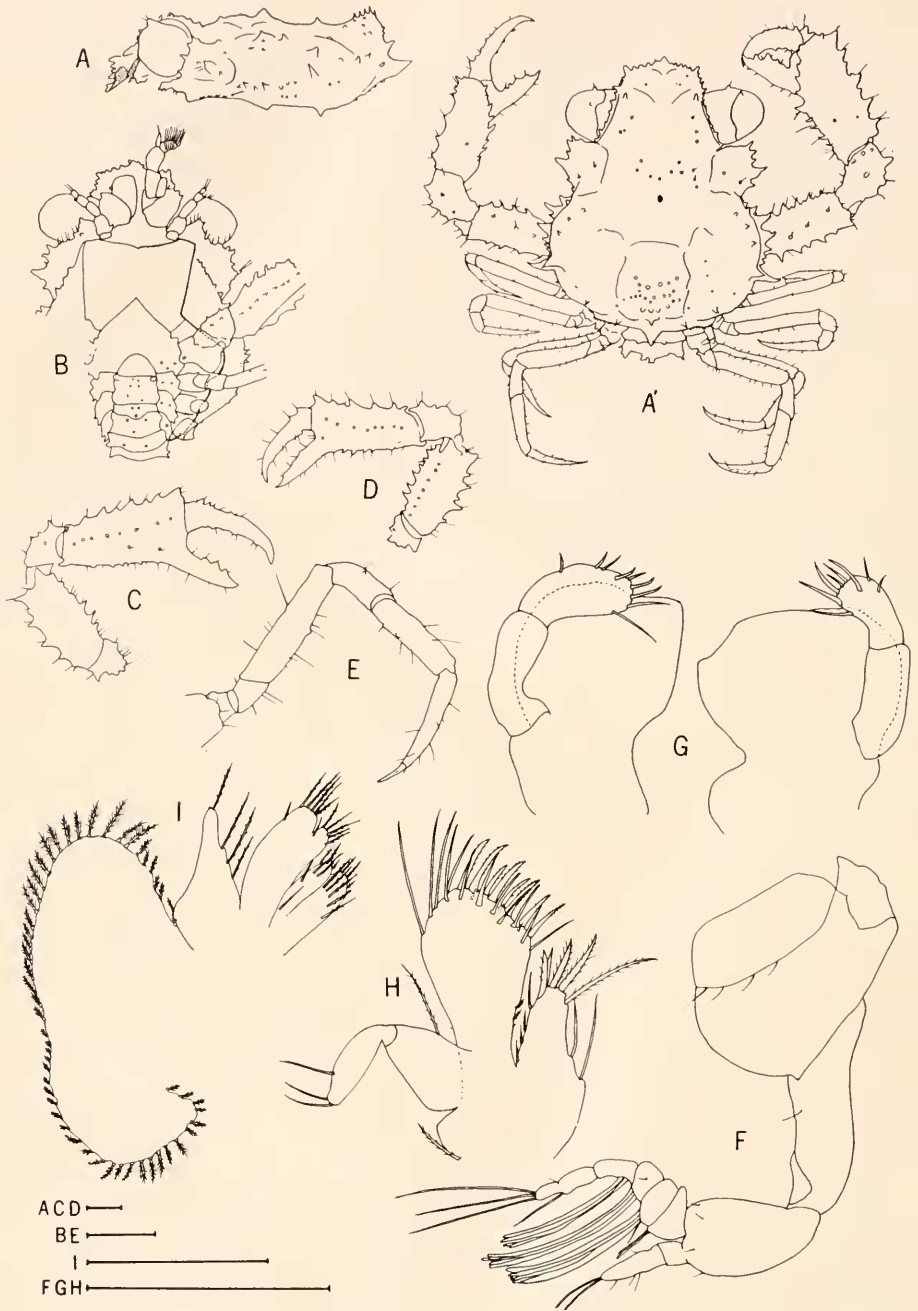


FIGURE 9. *Parthenope serrata*: First crab; A, lateral view of carapace; A', dorsal view; B, ventral view of carapace; C, ventral view of right cheliped; D, ventral view of left cheliped; E, pereiopod 5; F, antenna 1; G, mandible; H, maxilla 1; I, maxilla 2. Bar scales represent 0.2 mm.

bud of anterior arthrobranch, and small bud of podobranch. Cheliped with two well laminated arthrobranches. Pereiopods 2 and 3 each with a pleurobranch.

Color: Carapace shaded pale yellow. Melanophores on carapace and appendages placed as follows: stippled over dorsal surface of carapace; on proximal portion of rostrum at interorbital area; on posterior base of cardiac spine; on dorsal and inferior side of each branchial postero-lateral spine; on peduncle of eye; on first segment of peduncle of antenna 1; on coxopodite, meropodite and propodite of pereiopods 2-5; and on ischiopodite of maxilliped 3. Melanophores on cheliped as follows: two at base of hiatus, two at proximal portion of propodite, one at carpopodite, three small ones at meropodite; paired on ventral side of abdominal somites 2-6. Basipodite of pleopods on somites 2-6 and telson each with a faint melanophore and red chromatophore.

First Crab (Figs. 9, 10)

Carapace: Length approximately 1.70 mm; width 1.48 mm. Depth of carapace at cardiac region slightly greater than at gastric region. Medial portion of rostrum depressed into groove. *Abdomen:* Seven-segmented. No marked locking mechanism between it and thoracic sternum. *Antenna 1:* Dorsal surface of peduncle cup-shaped, well calcified with several hairs, acting as ventral floor of eye stalk. *Antenna 2:* Flagellum less calcified than peduncle, with seven segments. *Maxilla 1:* Endopodite segmentation obscure. Plumose seta from second zoeal stage still present on lateral margin, proximal to endopodite. *Maxilla 2:* Scaphognathite now with approximately 52 plumose setae. *Maxilliped 1:* Endopodite hatchet-shaped, apparently one-segmented. *Maxilliped 2:* Epipodite still small with two terminal hairs. *Maxilliped 3:* Ischio-basipodite cleavage slightly marked, with serrated ischiopodite medial margin. *Pereiopods:* Lateral margins of cheliped strongly serrated as in adult. Right cheliped, as in megalopa, much larger than left. *Pleopods:* Buds of subsequent crab stage pleopods 2-5 apparently present, but hard to detect.

Gills: Appear on appendages as follows: Maxilliped 2 with elongated bud of epipodite bearing one or two terminal hairs, and elongated podobranch bud. Bud of arthrobranch not apparent in this stage but is observed in second crab stage. Maxilliped 3 with well laminated posterior arthrobranch, and slightly laminated bud of podobranch and anterior arthrobranch. Cheliped with two well laminated arthrobranches. Pereiopods 2 and 3 each with a pleurobranch.

Color: Minute melanophores quite densely spotted on carapace, and on third maxilliped. Chelipeds, pereiopods 2-5, and proximal portion of antennae with small melanophores. Paired melanophores on external side of abdominal somites 2-6.

REARING RESULTS

Two broods from different ovigerous females collected at the same time and locality have been reared. Although the morphological study was based on material from the two broods, the present rearing results are of the brood which hatched on 4 April 1965. An ovigerous female (carapace length 17.2 mm; carapace width including lateral spines 24.5 mm) produced approximately 3900 zoeae in one brood.

Figure 11 illustrates survival and mortality of the animals reared at 25° C including the individuals which molted into megalopa after five zoeal stages. A little less than one half of the initial population molted into second zoea. After



FIGURE 10. *Parthenope serrata*: First crab; A, antenna 2; B, maxilliped 1; C, maxilliped 2; D, maxilliped 3. Bar scale represents 0.2 mm.

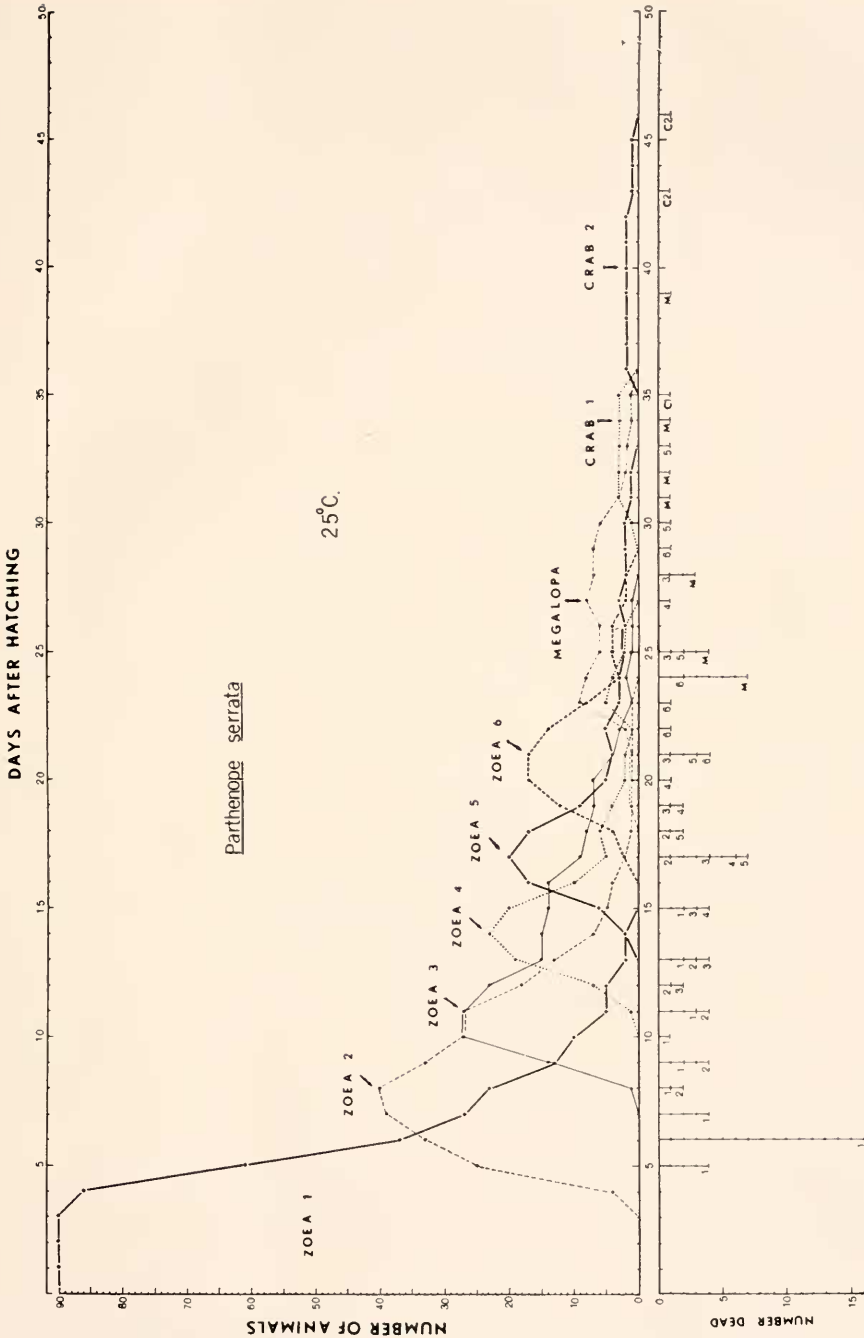


FIGURE 11. *Parthenope serrata*: rearing record at 25° C. The horizontal scale represents days after hatching. The vertical scale represents number of animals. The lower figure indicates number of deaths per day. The symbols 1 to 6, M, c1 and c2 represent, respectively, zoea 1 to zoea 6, megalopa, crab 1 and crab 2 stages.

the second zoeal stage, the number of individuals surviving into succeeding stages gradually decreased. Approximately one-ninth of the initial population reached the megalopa stage, but mortality in the megalopa stage was high. In this rearing none of the megalopae which had passed through five zoeal stages molted into the first crab stage. Three individuals out of the initial zoeal population of 90 reached the first crab stage in about 30 days after hatching and two individuals developed into the second crab stage. Among the larvae of this brood reared in 20° C two individuals reached the first crab stage in about 45 days; one individual reached the second crab stage but died immediately after molting.

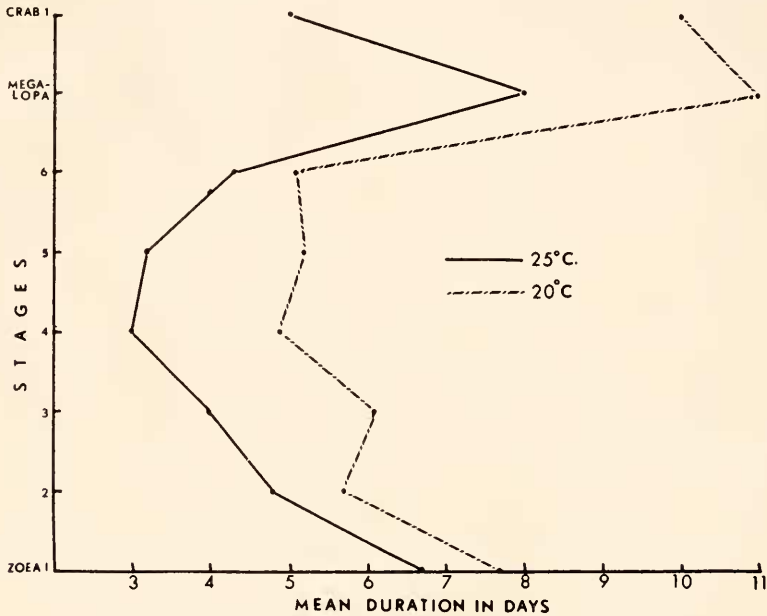


FIGURE 12. Duration of the larval and post-larval stages of *P. serrata* under two different temperatures.

The mean duration of each stage at 20 and 25° C is shown in Figure 12. The data of individuals reared at 20° C are based on an initial zoeal population of 45 individuals. The duration of the first crab stage at 20° C rearing is based on a single individual. The first zoeal stage at both temperatures had a greater duration than the succeeding stage. The majority of individuals which had a very prolonged first zoeal stage failed to complete development although some reached the intermediate zoeal stages. The general pattern of mean duration is quite similar in both 20° and 25° C although mean duration of intermediate zoeal stages was longer at 20° C than at 25° C. A prolonged duration of the megalopa stage is well marked in both groups. Provenzano (1968) observed a similar pattern in a study of anomuran larvae, and suggested that the prolongation of the metazoea and megalopa was probably due to reorganization of body structure. Robertson (1968) found a similar though less marked trend in his

TABLE I

Comparison of characters of first zoeal stage of Parthenopidae of known parentage

Species	<i>Parthenope serrata</i> H. Milne Edwards	<i>P. valida</i> De Haan	<i>P. massena</i> (Roux)	<i>P. angulifrons</i> Latreille
Reference	Present work	Aikawa, 1937	Heegaard, 1963	Heegaard, 1963
Dorsal spine	Much longer than carapace depth, tapers distally, bends posteriorly	Almost equal to carapace depth, tapers distally, bends posteriorly	Much longer than carapace depth, tapers distally, bends posteriorly	Much longer than carapace depth, stout, and blunt, somewhat straight
Rostral spine	Long, pointed	Long, pointed	Long, pointed	Long, pointed
Lateral spine	Fairly long	Short (?)	Fairly long	Fairly long
Postero-lateral processes on somites 3-5	Elongated projection, pointed	No projection, not pointed	Elongated projection, pointed	No projection, not pointed
Telson	Lunate	Lunate	Lunate	Slightly lunate
Spine on telson fork	1 dorsal spine only	1 dorsal only	1 dorsal spine, 1 lateral seta	1 dorsal spine, 1 lateral seta
Exopodite of antenna 2	1-segmented, 2 terminal spines	1-segmented, 2 terminal spines	2-segmented, 2 terminal spines	1-segmented, tapers distally with 2 subterminal spines
Endopodite of maxilla 1 (seta dist.) (seta prox.)	2-segmented, (2-4) (1)	2-segmented (2-4) (1)	3-segmented (2-4) (0)	3-segmented (2-4) (0)
Medial margin of endopodite of maxilla 2 (setae)	3 processes (2,2,3)	2 processes (?) (2,3+2)	3 processes (2,1,2)	2 processes (2,4)
Endopodite maxilliped 2	3-segmented	3-segmented	1-segmented (?)	2-segmented (?)
Locality	Florida, U. S. A.	Japan	Mediterranean	Mediterranean

study of phyllosomas of the lobster, *Scyllarus americanus* (Smith). The marked prolongation of the megalopa stage has been seen in the larval development of majid crabs which have only two zoeal stages (Yang, 1967).

DISCUSSION

The number of zoeal stages in development of the Parthenopidae has been in question for a long period. After noting that Cano described three zoeal stages, Lebour (1928, page 555) predicted that "there probably are four or five." Bour-

dillon-Casanova (1960) also assumed that the Parthenopidae had more than two zoeal stages.

Table I is constructed from the major anatomical distinctions and similarities among *P. serrata* and three species of parthenopid first zoeae of known parentage reared by Aikawa (1937) and Heegaard (1963).

There are some apparent character differences among the four reared species of parthenopid zoeae. However, there are unique zoeal characters which allow the larvae to be identified as parthenopids. These are summarized from the four species plus *Parthenope (P.) agona* and *Solenolambrus typicus*, also reared by the author (Yang, unpublished):

1. The carapace has well developed dorsal, lateral and rostral spines.
2. The outline of the telson is lunate with a "dorsally located spine" on each fork. A minute hair-like lateral seta is sometimes present.
3. Lateral knobs are present on abdominal somites 2-3.
4. The forehead protuberance is well developed as in most majid zoeae and the postero-dorsal knob of the carapace also appears to be present in the majority of parthenopids studied.
5. The endopodite of maxilliped 2 appears to be three-segmented with a disto-medial seta on the two proximal segments.

The carapace of the first zoeae is more or less spherical with long dorsal, rostral, and lateral spines. As zoeae molt to the subsequent stages, the distance between the anterior part of the eye and the basal part of the dorsal spine increases. The length of the dorsal and lateral spines rapidly decreases in proportion to the carapace size as does the rostral spine, while carapace height is also reduced at each subsequent stage. The dorsal spine thickens basally and shifts posteriorly. Thus, the distance between the posterior base of the dorsal spine and the postero-dorsal margin of the carapace decreases. At the sixth (last) zoeal stage, the carapace is remarkably depressed with shorter dorsal and reduced lateral spines and broader rostral spines. Thus, the carapace form becomes similar to that of the megalopa. A *Parthenope* megalopa retains the lateral spines of the zoeae on the branchial region. The so-called dorsal spine of the zoeal stage is a cardiac spine. This gradual change of shape is also seen in the zoeal stages and megalopa of *Callinectes* illustrated by Costlow and Bookhout (1959), and among other long-zoeae-stage crabs. Further, this shifting of the zoeal form into the megalopa is clearly observed in *Stenorhynchus seticornis* (Herbst) and *Rochinia hystrix* (Stimpson), both having but two zoeal stages (Yang, 1967).

Costlow (1965), and Rice and Provenzano (1966) reviewed the variability in larval stages of decapod larvae. In the present study, in one rearing of *P. serrata* at 25° C, zoeae developed into the megalopa stage. Thirteen of these molted from the fifth zoeae to megalopa while eleven molted from the sixth zoeae. Of the former, ten individuals died during or immediately after molting and three died later. Of those produced after 6 zoeal stages, two megalopae subsequently developed into crabs.

In the fourth zoeae of the five-staged series there are nine and ten natatory setae on maxillipeds 1 and 2, respectively. The fifth zoea of these series each have ten natatory setae on maxillipeds 1 and 2. The five-staged zoeae have a well-developed endopodite on antenna 2 and pleopods buds at the fifth stage, and the length is similar to the normal six-staged zoeae, but the development of

antenna 1 appears to be poor without an inner-flagellum bud, and with only two rows of aesthetascs.

In normal six-staged zoeal development, the inconsistent number of the plumose natatory setae was mentioned earlier. This variability of number of natatory setae is also reported by Yatsuzuka (1957) for *Portunus pelagicus* (L., as *Nep-tunus pelagicus*) and five other species of crabs.

I studied the larval and postlarval development of more than twelve species of Majidae from hatching, and determined that the zoeae of the Parthenopidae, which have Brachyrrhynchan zoeal characters, are easily distinguished from the majid zoeae in the following respects:

1. Six zoeal stages are observed in *P. serrata*, whereas in the true majid crabs the number of zoeal stages is apparently fixed at two, reflecting precocious or abbreviated development. The early zoeae of *P. serrata* and of the other Parthenopidae discussed above are alike in their anatomy, which is of a type characteristic for crabs with multi-zoeal development.

2. The zoeae of the Parthenopinae have dorsal, rostral, and lateral spines on the carapace. In general, dorsal and rostral spines are seen in the true majid zoeae. In the zoeae of the Inachinae (Majidae) only a dorsal spine is present.

3. The telson of the zoeae of the Parthenopinae is lunate with a spine located dorsally on each fork. In the Majidae this spine is lateral.

4. The exopodite of antenna 2 differs from that of general majid zoeae in having 2 terminal instead of 2 subterminal spines, plus a well developed endopodite bud in the first zoeal stage.

5. The "anterior seta" (Bourdillon-Casanova, 1960), present in the majid zoeae, is wanting in the zoeae of Parthenopinae.

Lebour (1928), discussing parthenopid zoeal characters, stated (page 555), "They are more like Cancridae, having all the carapace spines, antennae like *Portunus* (actually *Macropipus*), and only one lateral spine on the telson. If these larvae be correctly identified and representing the Parthenopidae, then this family does not agree with Majidae in any way, and is an exception among the Oxyrrhyncha." Aikawa (1935) merely mentioned that the zoeae of the Parthenopidae are remarkably close to those of the Cancridae, and later he placed the zoeae of the Parthenopidae into a group of the Cancridae (Aikawa, 1937).

Although both parthenopid and cancrioid zoeae share many zoeal features, the cancrioid zoeae of known parentage described by Lebour (1928), Aikawa (1937), Fagetti (1960), Mir (1961), and Pool (1966) show a remarkably different type of telson compared to that of the Parthenopidae. The cancrioid zoeae possess lateral-knobs only on abdominal somite 2.

Lebour (1944) gave a brief description and illustration of a megalopa which she attributed to a species of *Parthenope*, based on the elongated chelipeds and lack of "feelers" on the dactyl of pereopod 5. She mentioned that her megalopa also had lateral spines on abdominal somites 3-5, and the pleopod on somite 6 bore numerous spines. There are no such features in *P. serrata*. The elongated rostral spine and the posteriorly elongated cardiac spine of megalopa she examined are somewhat similar to *P. serrata*.

Lebour (1928, page 490) stated, "The presence of feelers on the last joint of the last legs cuts off the Brachyrrhyncha (with exception of Pinnotheridae) from the Oxyrrhyncha and from *Ebalia*. . . ." Gamō (1958) said that the number

of feelers in megalopa of eight species of Grapsidae ranges from three or four. There is only one feeler on the megalopa of *P. serrata*. Its tip is not serrated.

The megalopa of *P. serrata* can be distinguished from majid megalopae by the following:

1. In *P. serrata* there is a smooth feeler on the dactyl of pereopod 5; none in majids.

2. There are no knobs, projections or modifications on the distal portion of the basal article of antenna 2 in *P. serrata*. There are more flagellar segments than the four that occur in majid megalopae.

3. The first segment of the peduncle of antenna 1 in *P. serrata* is inflated; its dorsal surface is flattened and concaved. This serves as a partial support of the eyestalk.

4. The gills are much better developed, having the elongated bud of the future podobranch and a bud of the epipodite on maxilliped 2. This is characteristic of the megalopae of multizoeal crabs (Yang, 1967).

The following characters distinguish the first crab stage of *P. serrata* from those of majid crabs:

1. In the first crab of *P. serrata*, the shape of the carapace is quite similar to that of the adult, as in the first crabs of some majids (e.g., *Stenorhynchus* and *Epialtus*). However, the first crabs of other majids, e.g., *Libinia*, *Microphrys* and *Macrocoeloma* are very different from the adult.

2. The inflated and laterally expanded first segment of the peduncle of antenna 1 now serves as the ventral support of the eyestalk. In the early post-larval stages of majid crabs (Acanthonychinae, Pisinae, and Mithracinae), the knob on the disto-dorsal surface of the basal article of antenna 2 locks into the ventral socket of the rostrum. Thus, the basal article is the ventral support (floor) of the eyestalk in the majid crabs.

3. The podobranch of maxilliped 2 is well developed in the first, and second and the parent adult crabs. As in adult *Cancer* (cf. Pearson, 1908), it is located along the anterior margin of the branchial series.

The developmental pattern, as well as the character of respective zoeal stages of the Parthenopinae, is completely different from those of the Majidae.

The subfamily Parthenopinae in the Parthenopidae is much larger group (about 128 species) than the other subfamily Eumedoninae (about 25 species). The latter occur in the Indo-Pacific and the species are mostly commensal (Balss, 1957). The larvae of the Eumedoninae are not yet known and may differ from those of the Parthenopinae.

The Hymenosomatidae, one of three families of Oxyrhyncha, has unique zoeal characters (lack of the dorsal and lateral spines, and peculiar telson) which differ from those of the Majidae and the Parthenopidae (Gurney, 1938). Boschi *et al.* (1969) found three zoeal stages and the carapace with only a rostral spine in the hymenosomatid, *Halicarcinus planatus* (Fabricius) reared from hatching. Gurney (1942, page 282) suggested that the atypical zoeal characters of Hymenosomatidae, provide strong evidence against the inclusion of the Hymenosomatidae in the Oxyrhyncha. Thus, it is now evident that in the Oxyrhyncha the zoeal characters of each family differ from those of the others, indicating that the Oxyrhyncha, like the Oxystomata, are a heterogeneous group.

In the adult classification, most revisers of Oxyrhyncha as mentioned in the previous section placed the Parthenopidae under Oxyrhyncha. Flipse (1930) also dealt with the Parthenopidae as Oxyrhyncha in his Siboga Expedition Report. However, Dana (1851, pages 426-427) considered the Parthenopidae as intermediate between the Maiinea and the cancroïd crustacea because of the structure of the basal article of the antenna and the epistome, and Miers (1879, pages 635-636) stated that the Parthenopidae occupy a position almost intermediate between the rest of the Oxyrhyncha and certain Cancroïdea in respect to the structure of the antennae. Miers (1879; page 641) also assumed the nearest affinities of the Parthenopidae in Oxyrhyncha are in the direction of *Inachus* through *Inachoides*. Cano (1893, page 580) provided a scheme, based on the adult characters, showing that the Parthenopidae diverged from the Inachidae-Majidae line.

On the other hand, quite a few workers have not placed the Parthenopidae under Oxyrhyncha. Most of the authors did not give reasons for their classifications. Strahl (1862a and b) separated the Parthenopidae from Oxyrhyncha and grouped it with Calappidae on the formation of the basal article of the antenna. The structure and formation of the rostrum, cephalothorax, antennae and orbits caused Ortmann (1893; pages 412-413) to place the parthenopid group under Cyclometopa. Guinot (1966 and 1967), seeking a "parthenoxystomiene" line, suggested the parthenopid crab (*Aethra*) and some oxystomous crabs (*Osachila*, *Hepatus*, *Hepatella* and *Actaeomorpha*) be united, because of their adult morphological characters.

Clearly, the systematic position of the Parthenopidae, based on adult characters, is still in question.

The larval characters of the Parthenopinae are completely different from those of Majidae and Hymenosomatidae. Parthenopid larvae are different at least from the Majidae in the number of zoeal stages, the formation and pattern of antenna 2, and the gill formation. The larvae of the subfamily Eumedoninae are completely unknown. However, the larval characters of the Parthenopinae (*Parthenope*) strongly suggest a relationship to the Brachyrhyncha rather than to the Oxyrhyncha.

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SUMMARY

1. Larvae of an oxyrhynchous crab, *Parthenope* (*Platylambrus*) *serrata* (H. Milne Edwards), were successfully reared in the laboratory from hatching to the second crab stage on a diet of *Artemia* nauplii. Six zoeal stages, one megalopa and the first crab stage are described and illustrated.

2. Two series of larvae were reared at each of two temperatures, 20° and 25° C. The salinity ranged between 34 and 37‰. The mortality of the first zoeal stage reduced the initial population to less than half. The first crab stage was attained in approximately 30 days at 25° C, and in 45 days at 20° C, after hatching. The first zoeal stage and the megalopal stage showed more prolonged mean duration than intermediate stages and the pattern of mean duration was similar in both 20° and 25° C.

3. The major characteristics of four species of parthenopid first zoeae of known parentage are tabulated for comparison. The major distinctive characters of *Parthenope* larvae are presence of rostral, dorsal and lateral spines on the carapace, lunate telson with a dorsally located spine on each fork, normally six zoeal stages, and a smooth "feeler" at the tip of the fifth pereopod in the megalopa.

4. The number of zoeal stages and the morphological characters are compared to those of oxyrhynchous crabs. The larval characters suggest that Parthenopinae should be removed from the superfamily Oxyrhyncha and placed in the Brachyrhyncha.

LITERATURE CITED

- AIKAWA, H., 1935. Inachidae ka oyobi kinen-shu no zoea youchū no keitai [The zoeal morphology of the family Inachidae and allied species]. *Zool. Mag. (Dobutsugaku Zasshi) Tokyo*, **47**: 217-227.
- AIKAWA, H., 1937. Further notes on brachyuran larvae. *Rec. Oceanogr. Wks. Japan*, **9**: 87-162.
- ALCOCK, A. W., 1895. Materials for a carcinological fauna of India. No. 1. The Brachyura Oxyrhyncha. *J. Asiat. Soc. Beng.*, **64**: 157-291.
- BALSS, H., 1957. Abteilung Brachyura, Borradaile, 1907. Pages 1505-1672 in H. G. Bronns, Ed., *Klassen und Ordnungen des Tierreichs* 5 (1) 7.
- BORASCHI, L., 1921. Osservazioni sulle larve dei Crostacei Decapodi, Brachiuri e Anomuri. *Memorie R. Comitato Talassografico Italiano*, **87**: 1-32.
- BOSCHI, E. E., M. A. SCELZO AND B. GOLDSTEIN, 1969. Desarrollo larval del cangrejo *Halicarcinus planatus* (Fabricius) en el laboratorio (Crustacea, Decapoda, Hymenosomidae), con observaciones sobre la distribución de la especie. *Bull. Mar. Sci.*, **19**: 225-242.
- BOURDILLON-CASANOVA, L., 1960. Le Meroplancton du Golfe de Marseille: Les larves de Crustacés Décapodes. *Rec. Trav. Sta. Mar. Endoume Fac. Sci. Marseille*, **30**(18): 1-286.
- CANO, D. G., 1893. Sviluppo e Morfologia degli Oxyrhynchi. *Mitt. Zool. Sta. Neapel*, **10**: 527-583.
- COSTLOW, J. D., JR., 1965. Variability in larval stages of the blue crab, *Callinectes sapidus*. *Biol. Bull.*, **128**: 58-66.
- COSTLOW, J. D., JR., AND C. G. BOOKHOUT, 1959. The larval development of *Callinectes sapidus* Rathbun reared in the laboratory. *Biol. Bull.*, **116**: 373-396.
- DANA, J. D., 1851. On the classification of the Maioid Crustacea or Oxyrhyncha. *Amer. J. Sci., Ser. 2*, **11**: 425-434.
- FAGETTI, G. E., 1960. Primer estadio larval de cuatro Crustaceos Braquiuros de la Bahía de Valparaiso. *Rev. Biol. Mar.*, **10**: 143-154.
- FLIPSE, H. J., 1930. Die Decapoda Brachyura der Siboga-Expedition. VI. Oxyrhyncha: Parthenopidae. *Siboga Exped., Monog.*, **39**: 1-96.
- GAMŌ, S., 1958. On the post larval stages of two species of crabs of the subfamily Varuninae, Grapsidae, Brachyuran Crustacea. *Zool. Mag. (Dobutsugaku Zasshi) Tokyo*, **67**: 373-379.
- GARTH, J. S., 1958. Brachyura of the Pacific coast of America. Oxyrhyncha. *Allan Hancock Pacif. Exped.*, **21**: 1-854.

- GOURRET, P., 1884. Considérations sur la faune pélagique du Golfe de Marseille. *Ann. Mus. Hist. Natur. Marseille, Zool.*, 2(2): 1-175.
- GUINOT, D., 1966. Recherches préliminaires sur les groupements naturels chez les Crustacés Décapodes Brachyours. I. Les affinités des genres *Aethra*, *Osachila*, *Hepatus*, *Hepatella* et *Actaeomorpha*. *Bull. Mus. Hist. Natur., Paris*, 38: 744-762.
- GUINOT, D., 1967. Recherches préliminaires sur les groupements naturels chez les Crustacés Décapodes Brachyours. I. Les affinités des genres *Aethra*, *Osachila*, *Hepatus*, *Hepatella* et *Actaeomorpha* (suite et fin). *Bull. Mus. Hist. Natur., Paris*, 38: 828-845.
- GURNEY, R., 1938. Notes on some decapod Crustacea from the Red Sea, VI: Some brachyuran larvae. *Proc. Zool. Soc. London*, 108: 73-84.
- GURNEY, R., 1942. *Larvae of Decapoda Crustacea*. Ray Society, London, 306 pp.
- HEEGAARD, P., 1963. Decapod larvae from the Gulf of Napoli hatched in captivity. *Vidensk. Medd. Naturhist. Foren. Kjobenhavn*, 125: 449-493.
- HOLTHUIS, L. B., 1959. The Crustacea Decapoda of Suriname (Dutch Guiana). *Zool. Verh.*, 44: 1-296.
- LEBOUR, M. V., 1928. The larval stages of the Plymouth Brachyura. *Proc. Zool. Soc. London*, 1928: 473-560.
- LEBOUR, M. V., 1944. Larval crabs from Bermuda. *Zoologica*, 29: 113-128.
- MIERS, E. J., 1870. On the classification of the maioid Crustacea or Oxyrhyncha, with a synopsis of the families, subfamilies, and genera. *J. Linn. Soc. Zool.*, 14: 634-673.
- MILNE EDWARDS, H., 1834. Histoire naturelle des Crustacés, comprenant l'anatomie, la physiologie et la classification de ces animaux. In *Librairie Encyclopédique de Roret Volume I*, Paris.
- MIR, R. D., 1961. The external morphology of the first zoeal stages of the crabs, *Cancer magister* Dana, *Cancer antennarius* Stimpson and *Cancer anthonyi* Rathbun. *Calif. Fish Game*, 47: 103-111.
- ORTMANN, A., 1893. Die Decapoden-Krebse des Strassburger Museums. VII. Theil Abtheilung: Brachyura (*Brachyura genuina* Boas) II. Unterabtheilung: Cancroidea, 2. Section: Cancrinea, 1. Gruppe: Cyclometopa. *Zool. Jahrb. Abt. Sys. Oekol. Geogr. Tiere* 7: 411-495.
- PEARSON, J., 1908. Cancer. In *Liverpool Marine Biology Committee Memoirs XVI*. Williams and Norgate, London.
- POOL, R. L., 1966. A description of laboratory-reared zoeae of *Cancer magister*, and megalopa taken under natural conditions (Decapoda Brachyura). *Crustaceana*, 11: 83-97.
- PROVENZANO, A. J., 1968. The complete larval development of the West Indian hermit crab, *Petrochirus diogenes* (L) reared in the laboratory. *Bull. Mar. Sci.*, 18: 143-181.
- RATHBUN, M. J., 1925. The spider crabs of America. *Bull. U. S. Nat. Mus.*, 129: 1-693.
- RICE, A. L., AND A. J. PROVENZANO, 1966. The larval development of the West Indian sponge crab *Dromidia antillensis* (Decapoda: Dromiidae). *J. Zool., London*, 149: 297-319.
- ROBERTSON, P. B., 1968. The complete larval development of the sand lobster *Scyllarus americanus* in the laboratory, with notes on larvae from plankton. *Bull. Mar. Sci.* 18: 294-342.
- SAKAI, T., 1938. *Studies on the crabs of Japan. III. Brachygnatha, Oxyrhyncha*. Yokendo Publishing Co., Tokyo.
- STRAHL, C., 1862a. Über eine neue Species von *Acanthocyclus* Lucas, seine systematische Stellung und Allgemeines über das System der Dekapoden. *Monatsbericht Deutschen Akademie Wissenschaften Berlin*, (1861), 12: 713-717.
- STRAHL, C., 1862b. On a species of *Ruppellia*, Milne-Edwards, and the limit of the Brachyura. *Ann. Natur. Hist.*, 9: 299-303.
- WILLIAMS, A. B., 1965. Marine decapod Crustaceans of the Carolinas. *Fish. Bull. Fish. Wildlife Serv. U.S.*, 65: 1-298.
- YANG, W. T., 1967. A study of zoeal, megalopal, and early crab stages of some oxyrhynchous crabs (Crustacea: Decapoda). *Unpublished Doctoral dissertation, University of Miami*, 459 pp.
- YATSUZUKA, K., 1957. Study of brachyuran zoea (artificial rearing and development). Pages 571-590 in *Suisan Gaku Shūsei* (Fisheries Compilation). Tokyo University Press, Tokyo.